FORM AND GROWTH IN THE DEVELOPMENT OF A SCYPHOMEDUSA

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The nature and development of the scyphistoma and strobila of certain Scyphomedusae have been described a number of times, from various points of view.

Among the Semaeostomae, our knowledge of Aurelia and Chrysaora (including Dactylometra) is fairly complete, although correlations of form and size have not been emphasized. The other two forms that have been studied to some extent are Pelagia, the egg of which transforms directly into a medusa, and Cyanea. In the case of the Rhizostomae the developmental cycle is known for Cassiopea, Cotylorhiza and Nausithoë.

The present account is based upon a collection of scyphistomae and strobilae tentatively identified as those of *Cyanea capillata* Eschscholtz.

Source of Material

The material was part of an unlabelled collection in the Zoology museum at McGill University, a circumstance that adds an uncertainty of original site to the usual uncertainty of parentage of scyphistomae found in their natural habitat.

Fortunately, the internal evidence is decisive. The scyphistomae were attached to ascidians or to eel grass (*Zostera marina*) to which the ascidians in turn were attached. Fastened between some of the ascidians were several very young specimens of *Cucumaria frondosa*. The presence of the holothurian places the locale on the Atlantic coast north of Cape Cod. The ascidian is definitely identified as *Molgula provisionalis* Van Name, a species closely related to *M. manhattensis* and previously confused with it (cp. Van Name, 1945, p. 389). *Molgula provisionalis,* however, is recorded only from waters in the general region of Eastport, Maine, from Passamaquoddy Bay to Mount Desert. Since it is known that collections of this species of Molgula, attached to eel grass, have been made at St. Andrews Point in Passamaquoddy Bay, there is little doubt that the material is part of such a collection, and in any case there appears to be no doubt that these scyphistomae came from shallow water near the mouth of the Bay of Fundy.

Identification of Material

Identification of the genus and species is rather more difficult. The obvious suspects are *Aurelia aurita* and *Cyanea capillata,* since both of these are abundant in the region. *Dactylometra quinquecirrha* (a "Chrysaora") reaches the shoreline at Cape Cod, but is not reported from inshore waters of northern New England. The most northerly occurring rhizostomid of the Atlantic coast is *Rhopilema verrillii,* a southern form that occasionally strays into Long Island sound. The only

remaining form is *Phacellophora ornata*, another semaeostomid, which is known only from Eastport and the Bay of Fundy as two isolated records, by Verrill in 1869 and Fewkes in 1888.

The strobilae do not resemble those of Aurelia (cp. Percival, 1923) or Chrysaora (cp. Chuin, 1930), and while they are remarkably like those of the rhizostomids Cassiopea (cp. Bigelow, 1900) and Cotylorhiza (cp. Claus, 1892), it is not reasonable to assume the occurrence of an unknown rhizostomid in the region in question, nor to extend the range of Rhopilema from Long Island Sound through the five hundred miles of cold water north of Cape Cod. The alternatives remain Cyanea or Phacellophora, and the absence of any record of Phacellophora during the last sixty years makes it a most unlikely candidate. It is provisionally assumed, therefore, that our scyphistomae and strobilae belong to Cyanea, even though the somewhat brief earlier descriptions of the life cycle of Cyanea are significantly different from the account given here.

The Cyanea of the western Atlantic is *C. capillata* Eschscholtz. According to Mayer (1910), *C. arctica* Perón and Lesueur and *C. lamarckii* Perón and Lesueur are synonymous, or at the most are varieties of doubtful stability. The embryonic and early larval stages have been intensively studied by Hyde (1894) as *C. arctica*. Young scyphistomae were reared by L. Agassiz (1862) as *C. arctica* and by Perez (1920) as *C. capillata*. Planulae were reared in aquaria through the scyphistoma to the strobila and ephyra stages by Hargitt (1902 and 1910) as *C. arctica* and by Delap (1905) as *C. lamarckii*. The scyphistomae described by the above investigators might well be of one and the same species, but the strobilae are very differently described and in neither case do they conform at all closely with the one given here. Both Hargitt and Delap obtained planulae directly from known medusae, and the difference expressed in their descriptions must be due either to differences in culture conditions or to a genetic difference in the parent organisms. These differences will be discussed following the description of the present material, which in spite of the element of doubt will be assumed to be that of *Cyanea capillata*.

Growth of the Scyphistomae

Since there is no indication that long lateral stolons are formed, as in Aurelia, that could produce buds at a considerable distance from a parent scyphistoma, the minute individuals found in scattered and very isolated positions are assumed to be newly attached planulae. The possibility of migratory buds, however, is not excluded. Typical examples are shown in Figure 1, A–D.

The planula apparently attaches by its narrow end, and in some cases at least sends out two or three root-like processes of attachment (Fig. 1, A, B). Four tentacles appear around the developing manubrium, while four more are added, bringing the number to eight without significant change in size from the original state (Fig. 1, C, D). Eight new tentacles appear, raising the total to sixteen, again with little increase in the size of the whole.

At the same time a small bud protrudes from the wall of the hydroid at or near the junction of the body and stalk (Fig. 1E). Similar buds, appearing at the same site, occur in scyphistomae of all sizes (Fig. 1, G–J), although many scyphis-

tomae equally representative of all sizes were found without buds (Fig. 1F). The conclusion is that a series of such buds may be produced by an individual scyphistoma. The first appearance of a bud in a minute scyphistoma is in itself an expression of a local acceleration of growth, and it would be gratuitous to assume that this growth would become abruptly arrested and that the same bud would remain
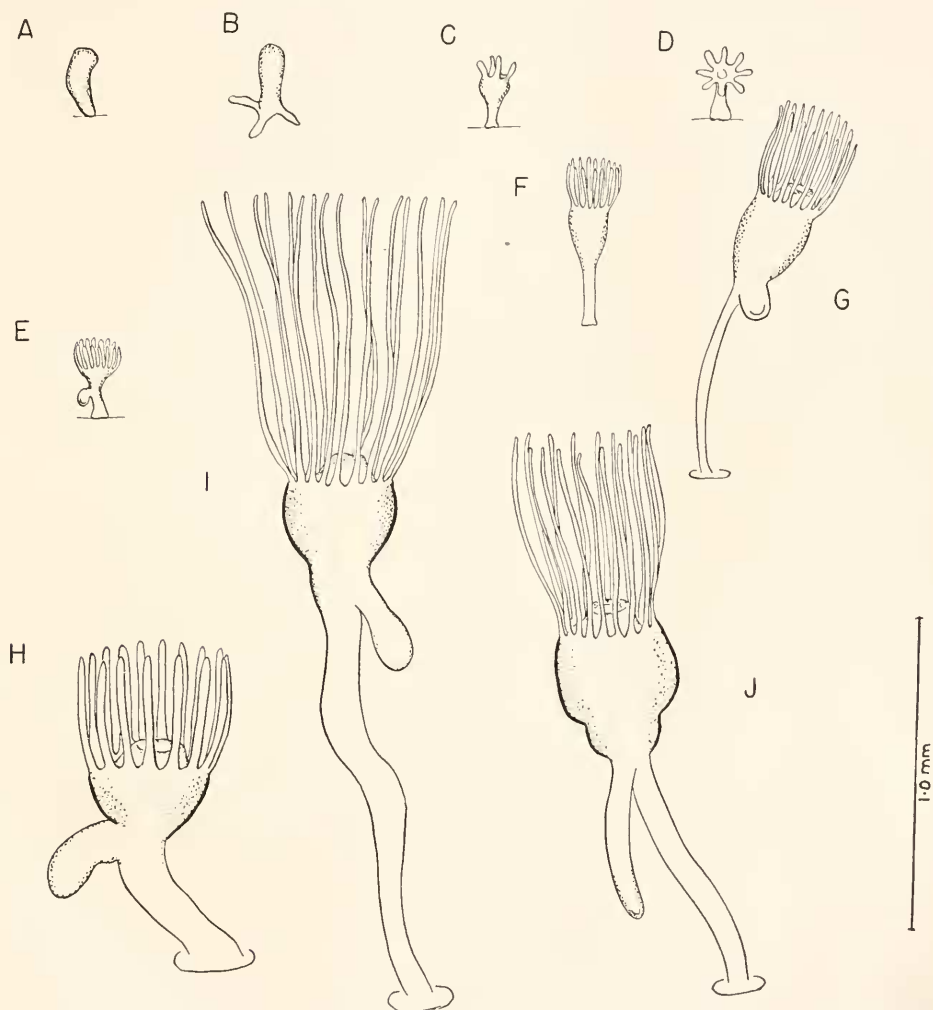

FIGURE 1. Growth and budding of scyphistomae of *Cyanea capillata*. A, B, attached planulae. C, 4-tentacle scyphistoma. D, 8-tentacle form. E, 16-tentacle scyphistoma with lateral bud. F, larger form without bud. G, H, I, J, older scyphistomae with buds.

but little changed in relative proportions in the large scyphistomae. It is more reasonable to interpret the conditions illustrated as being either the production of several buds successively from one site, or the production of but one bud, though at different stages of growth among different individuals.

In the great majority, the direction of growth of the bud is from the top of the stalk downwards towards the substratum. Growth of the bud is primarily stolonic, and is mainly by terminal proliferation of cells (cp. Fig. 1J). The largest scyphistoma of this type is shown in Figure 2B. No indication that such outgrowths extend to any distance has been found, and the occurrence of associations such as that shown in Figure 1, A and E, suggests that the buds grow down to become attached to the substratum close to the base of the parent, and constrict off from the parent at the point of origin.
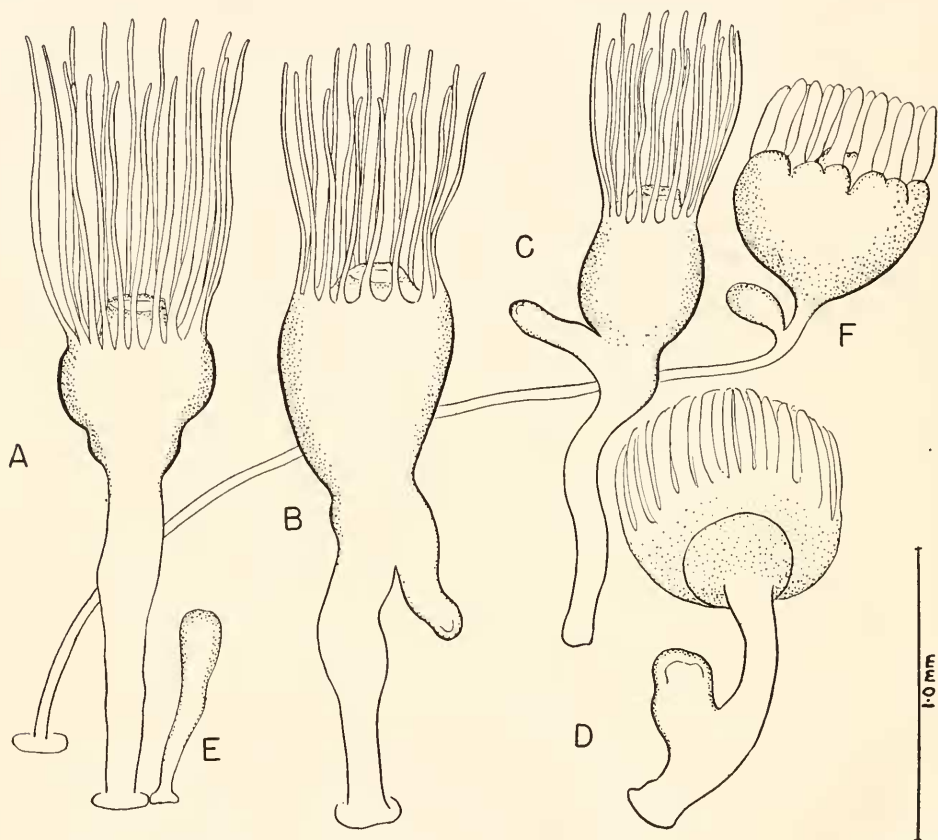

FIGURE 2. Fully grown scyphistomae of *C. capillata*. A, commencement of strobilation B, with bud directed downwards. C, D, with buds directed anteriorly. E, detached and attached bud at base of parent. F, metamorphosing scyphistoma with late bud.

In a minority of cases the bud grew upwards instead of downwards (Fig. 2, C, D) and in one case grew from the top of a long tenuous stalk that was bearing a metamorphosing scyphistoma at its end. Conditions such as these probably lead to those shown in Figure 3, A and B. In fact, Figures 2C and 3A might well be placed in sequence, the scyphistoma of Figure 2C having partially metamorphosed to become an ephyra in Figure 3A, the bud of Figure 2C having become a scyphistoma in Figure 3A, while the mutual relationship of the stalks remains unchanged.

On the other hand, the comparable stages of metamorphosis exhibited by the two heads of the individual shown in Figure 3B suggest the possibility that the division of the distal end preceded differentiation into scyphistomae, especially since the head that is somewhat the smaller is actually the more advanced, for only the eight interlobular tentacles remain. Such a condition seems more likely to arise
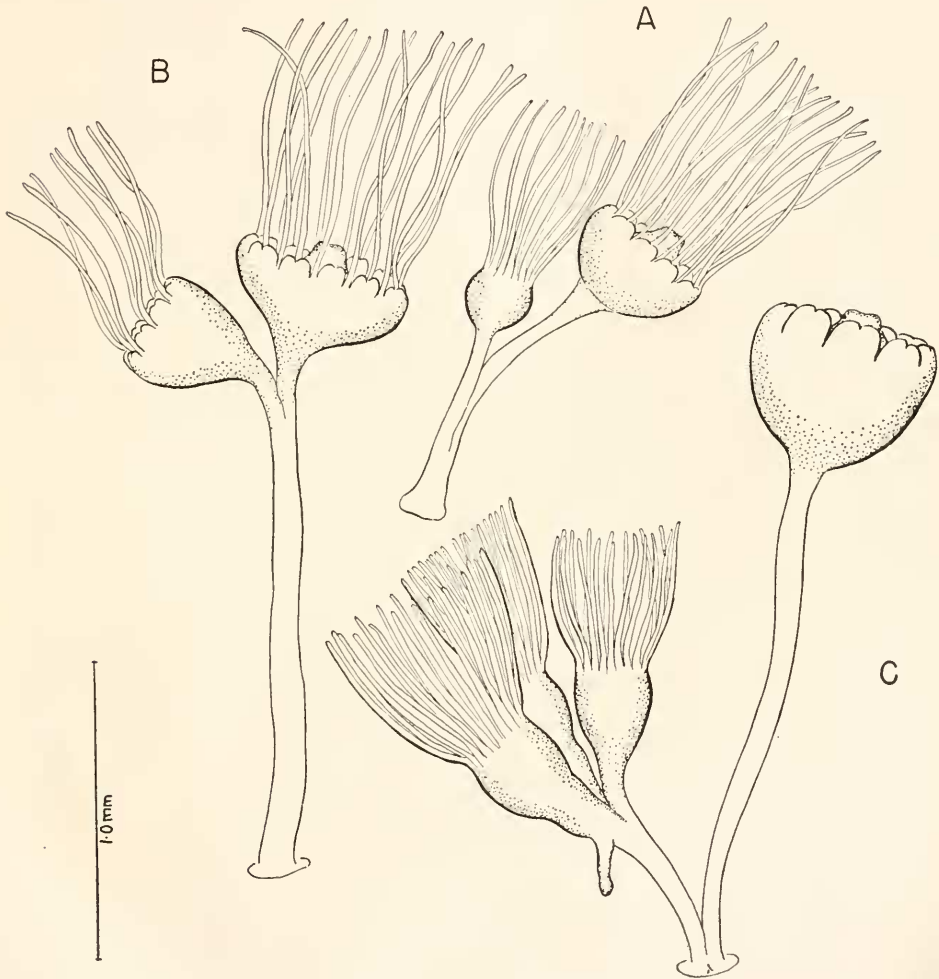

FIGURE 3. Retention and division of buds of *C. capillata*. A, bud forming scyphistoma attached to stalk of parent. B, double-headed strobila. C, strobila with three-headed scyphistoma attached to stalk base.

at the point of detachment of a bud from its parent than at the distal end of a newly attached planula. This is somewhat forcibly indicated by the example shown in Figure 3C. The parent scyphistoma is well advanced in its metamorphosis into an ephyra. The associated stalk may possibly have arisen from a bud similar to that seen in Figure 2D, but one arising even more proximally, or equally, if not more

likely, from a bud that grew downward from the usual site to become attached at the base of the parental stalk. In any case its distal end has given rise to three scyphistomae of approximately equal size. It does not seem possible that any one of the three could have given rise to the other two by budding, for there is too close an identity of size and form. In one of the three individuals a bud is growing downward, almost like a regeneration of an additional stalk to compensate for the multiplicity of heads.

Formation and Development of Strobilae

During the process of growth, the scyphistoma becomes progressively differentiated into stalk and head as in Figure 1I. In many cases metamorphosis into an ephyra occurs in a typical manner and purely as a monodisk. The head shortens and widens, eight of the sixteen tentacles resorb during the formation of the eight rhopalia, while somewhat later the eight interlobular tentacles are also resorbed. At the same time, the outer margin of the scyphistoma divides into eight lobes corresponding to the lappets of the future ephyra.

While in many cases a single ephyra may form from the head of a scyphistoma, in as many others, if not more, two or three ephyrae are produced in series. Whether one or more are to be formed is discernible from the contour of the scyphistoma before there is any other metamorphic indication, as in Figure 1J and 2A. In most cases, if not all, the interlobular tentacles are retained until shortly before the ephyra is set free (Fig. 3A). In no case have tentacles been seen in a developing ephyra that is second in line.

Three stages in the later development are illustrated by Figure 3, A, C, and E, representing the eight-tentacle stage (3A), all tentacles resorbed (3C), and the fully developed ephyra on the point of liberation (3C).

Cases such as the one shown in Figure 3B, in which two ephyra are almost at the same advanced stage of development, suggest that the ephyra probably grows to a certain critical size, when its development is functionally complete and it is ready to be set free, even though greater differences in size may be more evident at an earlier stage (cp. Fig. 3A). The individual shown in Figure 3D probably represents a second ephyra, the first having been liberated, and the same may be true for the primary individual in Figure 2C. Otherwise there is considerable variation in the time or size at which all tentacles become resorbed.

In all of the individuals with ephyrae, shown in Figure 3, there is present a relatively small basal swelling at the junction with the stalk, suggestive of a third ephyra. Marginal lobes tend to develop, though not in relation to any particular size (cp. Fig. 3A, 7D), and it is possible that an ephyra would have developed. The fact, however, that no individual has been found with three unmistakable ephyrae in process of formation may mean one of two things; either the third effort remains abortive, or else the first ephyra is always liberated before the third is definitely established.

It is notable that these third attempts at annular growth usually bear short tentacles in the lobular position (e.g. Fig. 3, C and E), possibly indicative of the re-establishment of the scyphistoma state.

A number of isolated stalks were found, of the same size as the largest bearing ephyrae, which possessed four distal tentacles as in Figure 3F. These may rep-

resent a return to the scyphistoma condition as is generally the case in Aurelia and Chrysaora, giving rise to another crop of ephyrae at some later time. On the other hand no scyphistoma was found that had a fully grown stalk and a head with either eight or sixteen tentacles. In our opinion such stalks as that illustrated are merely the final differentiation of the residual stumps after the ephyrae have been liberated, and in this form they do not give rise to further generations.

DISCUSSION

The essentially monodisk character of strobilation just described is much more reminiscent of the strobilae of the rhizostomids *Cotylorhiza tuberculata* (Claus, 1892) and *Cassiopea xamanchu* (Bigelow, 1900) than the polydisk strobilation described for *Cyanea lamarckii* by Delap (1905) at Valencia, and much more extreme than that of *Cyanea arctica* as described by Hargitt (1910) from Woods Hole. The question arises whether the differences indicate different parentage or a varying response to different conditions of growth.

Both size and shape appear to determine the type of strobilation, and since there is the possibility that the type may vary greatly with external conditions, it may be well to exclude Aurelia as a candidate somewhat more definitely. In the first place, a freshly liberated ephyra of Aurelia has a relatively shorter manubrium, gastral filaments much more remote from the manubrial base, and less suggestion of inter-rhopalial tentacles, than the ephyra of our present form shortly before liberation. Secondly, the manner of budding of the scyphistomae is markedly different. If the choice lies between Aurelia and Cyanea, as it appears, there is little doubt that Cyanea is the parent form.

The growth of a scyphistoma up to the time of liberation of an ephyra is divisible into three phases. The first concerns the transformation of the planula into a 16-tentacle scyphistoma. This phase has been intensively studied in relation to the manner of origin of the stomach pouches and the order in which the tentacles arise. Neither of these features greatly concerns us here; our main interest lies in the manner of growth and budding of the scyphistoma, and in the strobilation to form ephyrae.

The second phase, the growth of the 16-tentacle scyphistoma, is associated with the production of buds. In both the rhizostomids, Cotylorhiza and Cassiopea, buds arise one at a time from the scyphistoma body wall above the apex of the stalk. The buds break free, are ciliated and free-swimming, but they eventually settle and become attached by their original outer end.

In the semaeostomids Aurelia and Chrysaora, buds are formed initially as lateral outgrowths from the body wall near the base of the scyphistoma. They grow out as stolons for a considerable distance before becoming attached (Fig. 5B) either to give rise to a new scyphistoma at the point of attachment, or to one or two scyphistomae at some place between origin and attachment. The connection with the parent is finally broken.

In our Cyanea the buds arise from a site equivalent to the point of origin in Cotylorhiza and Cassiopea, but grow longer and downward to become attached basally by the time separation from the parent takes place. In both types, however, the scyphistoma head grows from the upper end of the bud. It is therefore intermediate in character between that of Aurelia and Cassiopea. The three kinds
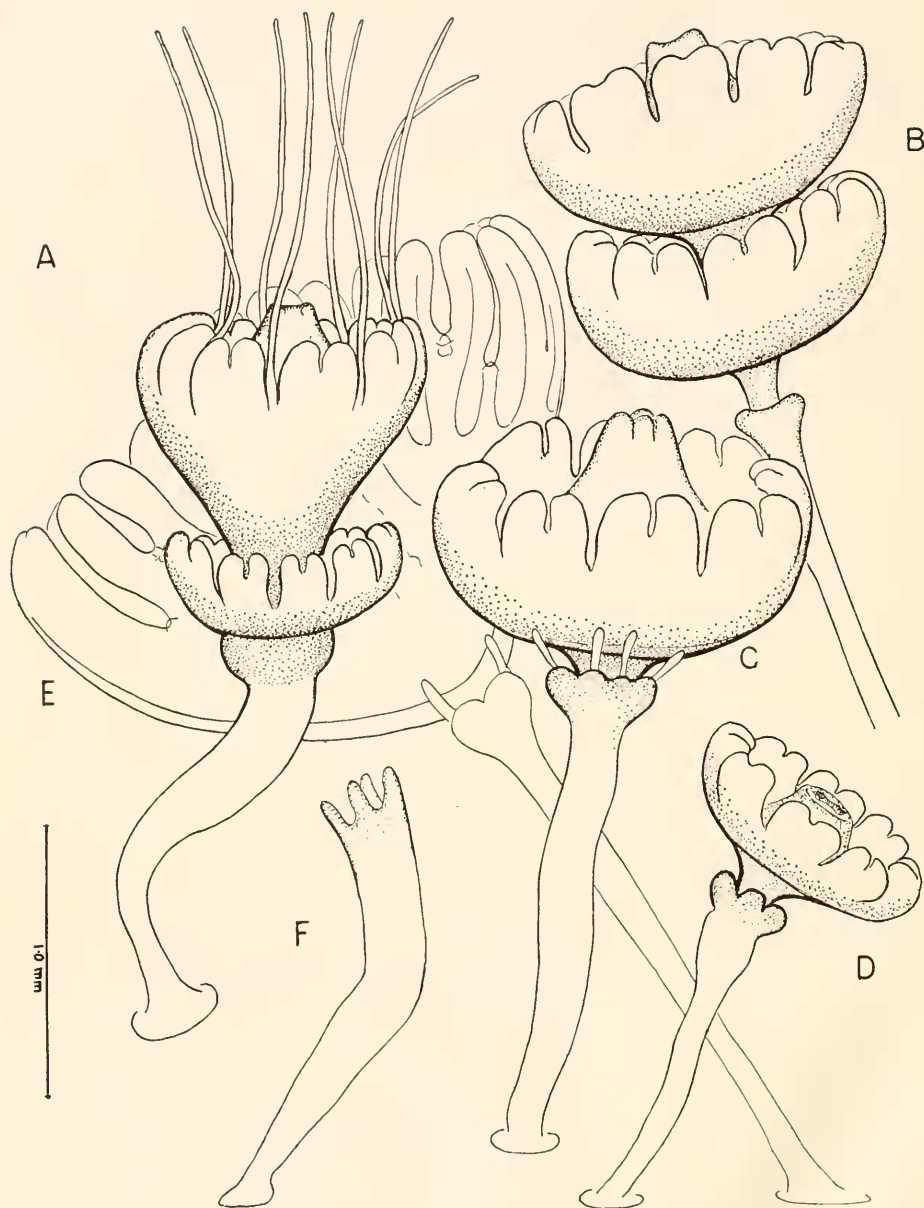
FIGURE 4. Strobilae of *C. capillata*. A, strobila with two ephyra and possible third. B, strobila with two equalized ephyrae. C, strobila with advanced ephyra and a potential second bearing scyphistoma tentacles. D, strobila with second ephyra well developed and a potential third. E, ephyra on point of liberation. F, post-strobila stalk with four tentacles.

of buds are essentially the outcome of two variables, the direction of outgrowth and the intensity of growth. Subsequent development depends upon the orientation of the outgrowth, and a new scyphistoma always arises from an upper surface, whether it be the distal or proximal end of an outgrowth or from some point on its side wall.

The question of monodisk or polydisk strobilation concerns both size and shape, both of which are expressions of growth. In monodisk development, growth in the basal part becomes progressively linear and apparently becomes arrested, while anterior growth becomes progressively transverse. Between the two regions there is a steep growth gradient producing a comparatively abrupt transition from head to stalk.

In contrast to this, the scyphistoma of Aurelia exhibits no such differentiation, and both transverse and linear growth occur throughout, so that while growth in length of the whole is the greater, transverse growth continues in basal as well as anterior regions. A large scyphistoma is therefore not very different in shape from a small one.

Shape is probably one of the main factors in determining the nature of strobilation. Constrictions carve off the shallow saucer-like discs of the scyphistoma to form ephyrae, and whether one, two, or many such discs can be produced is mainly a matter of the shape of the whole and the extent of growth occurring at the various levels. In this light, the difference between monodisk and polydisk strobilation is primarily a difference in the extent to which significant transverse growth can be maintained along the antero-posterior axis of the scyphistoma (cp. Fig. 2A, 5C). This activity may well vary with different conditions of temperature and food supply.

The scyphistomae reared by Delap grew steadily through summer months, apparently without producing buds, in each of two successive years, and in each year strobilated to form eight to eleven ephyra in late winter when the temperature fell below 45° C. The scyphistomae were abundantly fed with small planktonic organisms throughout the whole period. Those reared by Hargitt were fed even more concentratedly, at relatively high temperatures, and grew to the strobila condition with astonishing rapidity. One to five ephyrae were produced, with an average of three to four. Hargitt states that buds were seen but were extremely rare. Fortunately Delap gives the scale of her drawing of the strobila, so that a comparison of actual size is possible. Her polydisk strobilae are approximately three times the height of ours, and have no sharp division into stalk and head.

Our own scyphistomae were without doubt collected during the summer or late spring, and in Passamaquoddy waters would accordingly be developing at low temperatures (below 50° C.), even though maximum for the region. Growth would be relatively slow at the prevailing temperature and the food supply would probably fall far short of the degree of forced feeding employed by Hargitt and Delap.

The form of the sessile phase of the Hydromedusae responds sharply to varying conditions of temperature and food supply (Berrill, 1948, 1949) and it would be expected that the scyphomedusae would also react, in their own way. Differences in relative growth rates, however, may very well be inherited within the limits of a single species, and different races of *Cyanea capillata* may vary in the quantitative growth response their respective scyphistomae make to changing external conditions.

SUMMARY

The developmental cycle of a scyphomedusa, probably *Cyanea capillata* Esch-scholtz, is described, with emphasis upon the correlation of size and form.

The nature of the budding process, giving rise either to free buds or to double-headed forms, is described.

An analysis of monodisk and polydisk strobilation is given in terms of growth, size and shape.

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